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PATTERN IN THE DOG

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INTRODUCTION

Among psychologists, interest in behavior related to maturation has been continuing and widespread. This interest has sometimes provoked energetic controversies, as in the case of 'instinct' studies of earlier decades. Some areas of study, while offering numerous theories or hypotheses, have proceeded with serene but unflagging interest. Dextrality studies are an illustration of investigations in this latter area. But in all instances the opinion of those who study behavior related to maturation appears to be that their work is basic.

Many experimental investigations have concerned learning and its relationship to maturation. The work of Dennis (15) and Hilgard (17) with children are representative examples. In the case of animal work, Shepard and Breed (29) with their control over practice in the pecking of chicks gave impetus to a lengthy series of similar studies by many investigators.

Relatively few are studies dealing with behavior dependent upon maturation alone. The work of Coghill (13) in demonstrating how the extent of nervous development in *Amblystoma* is related to stages in swimming is a frequently quoted example. Another classic illustration is Carmichael's study (12) of swimming in tadpoles.

A field of current interest and expanding study concerns the role of hormones in relation to maturation and behavior. While most research in this area has been directed at copulatory behavior, a

¹ Condensed from a dissertation submitted in partial fulfillment of the requirements for the degree of doctor of philosophy in the University of Michigan (1942). The author wishes to acknowledge the friendly guidance of Professors J. F. Shepard, W. B. Pillsbury, W. C. Olson, B. D. Thuma, and L. R. Dice, all members of the doctoral committee. The Director and staff of the University of Michigan Laboratory of Vertebrate Biology are also to be thanked for providing the laboratory space required for this study.

number of more recent investigations have examined other behavioral items. Historically, Brown-Sequard (10) is probably responsible for the general interest in hormone activity. He injected testicular extracts in himself and experienced a marked increase in vigor and alertness which he concluded was due to the extract. Steinach (30) showed that the copulatory clasp reflex in male bullfrogs was abolished by castration and subsequently restored by the injection of testicular extracts. Stone (33) found that copulatory activity in the male rat waned after castration and that this activity was restored after injection of testosterone propionate, a male sex hormone. Ball and Stone (1, p. 1221) induced masculine behavior in female rats by means of testosterone propionate. Ball (4) found that the sex activity of four out of six male rats castrated when 4 months old was raised beyond the castrate level by injections of female sex hormones. Ball (5) also found male sex hormones administered to normal female rats resulted in a considerable increase in masculine sex behavior during the period of hormone injections and a rapid decrease in masculine behavior after the injections were stopped. Engel (16) found that the copulation pattern of castrated male rats was restored by the injection of hormones obtained from horse urine. Noble and Zitrin (24) administered testosterone propionate to young male chicks and estradiol benzoate, a female sex hormone, to female chicks. The treated male chicks crowed when about four days old and, when 15 days old, gave a complete, adult copulatory 'treading' response (the usual age for the appearance of this pattern is $4\frac{1}{2}$ months). The females to which estrogens were administered gave the female 'squatting' response to copulating males when about 20 days old. Using a hurdle box and observation cage, Seward (26) found castrated male guinea pigs revealed a gradual decline in crossings to reach a female, but that the number of crossings rose after testosterone injections.

In addition to the studies which have primarily been concerned with copulatory activity, there have been several investigations of hormonal action and maternal behavior. Kunde, D'Amour, Carlson, and Gustafson (20) produced lactation and maternal behavior in rats by estrin injections. Seward and Seward (28) obtained data which suggested that hormone activity was of prime significance in maternal behavior of guinea pigs. Hoskins (18, p. 184 f.) cites examples of the activity of the anterior pituitary lobe product *prolactin* in producing brooding of fowl, nesting of fish, and the adopting of mice, rabbits, and even squabs by young female rats.

Other studies have examined less specific behavior items or employed less direct control over hormones in relation to behavior. Anderson (2) found histological differences in certain endocrine glands

of various breeds of dogs and suggested (p. 648) that behavior peculiar to breeds of dogs ". . . might be dependent upon differences in glandular activity and quality." Beach (8) found a complete masculine copulatory pattern in some untreated female rats. He suggested (p. 140) that excessive androgenic activity of the ovaries or adrenals might be a causative factor.

A behavior item which has much to commend it from the standpoint of experimental investigation is micturition behavior of the dog. Micturition activity in dogs offers a sharp behavioral distinction between the sexes. All normal adult males elevate the leg when urinating, while normal females do not. Also, the response of the male is clear-cut and thus can be readily studied by methods such as photography, isolation, delay, etc. A further advantage is that studies of this behavior item might provide data useful for theoretical considerations of sex differentiated behavior. The urination pattern in the male suggests trial and error learning; yet maturation appears to be involved in that normal puppies never elevate the rear leg when urinating. Also, because of the sex difference in this behavior, hormone activity is a possible factor.

PROCEDURE

Twenty-two animals, 16 males and six females, were employed in the study. Ten animals from three litters were secured from farms when between one and three months old. Eleven animals from two litters were born under laboratory control, and thus had contact only with members of their own litters and the dam. The remaining animal was about 10 years old when secured from a metropolitan dog pound. A number of other animals were used for observation but were not placed under experimental conditions. All experimental animals appeared to be in good health when secured. The largest dogs were about the size of Airdales; the smallest were about the size and appearance of Dachshunde.

The dogs were housed in an isolated, wooden, double-walled structure which had two fenced-in exercise yards. The temperature in the building varied from 41° to 83° F. during the year of the study. The animals were kept in cages, usually several littermates to a cage. The cages were so constructed that the animals could not see other animals in nearby cages except when they were being carried to the exercise yard. Dogs undergoing hormone treatment were placed alone in a cage.

The animals were initially placed on a diet of canned and dry dog food and, up to the age of 14 weeks, condensed milk was included. Twice a week each animal was given 5 cc. of codliver oil. This diet was later found to be inadequate and raw beef, condensed milk, and codliver oil were substituted. This temporary diet inadequacy will be considered later. Water was supplied daily for a four hour period only. It was found that withholding water overnight and then permitting the animals all the water they desired during the observation period usually resulted in their urinating when placed in the exercise yard.

The animals were usually placed in the exercise yard with their littermates when observed, although observation of a single animal occasionally was employed. Each dog was observed on alternate days. Once each week a photographic record with a 16 mm. motion-picture camera was made of urination activity. Frames from these records were enlarged and used for the accompanying figures. Because camera 'angles' were not equally revealing for all dogs, there has necessarily been selection in the choice of figures.²

² Additional photographs are included in the thesis filed under the title of this article at the University of Michigan. Also, the experimental procedure is given in greater detail.

Practice in the delayed animals, 3b and 4d, was controlled by placing the dogs on a treadmill inside a narrow cage. Slings were placed under the chest, abdomen, and hind legs (Fig. 1). This arrangement permitted the animal to move his legs in a forward direction on the treadmill; how-

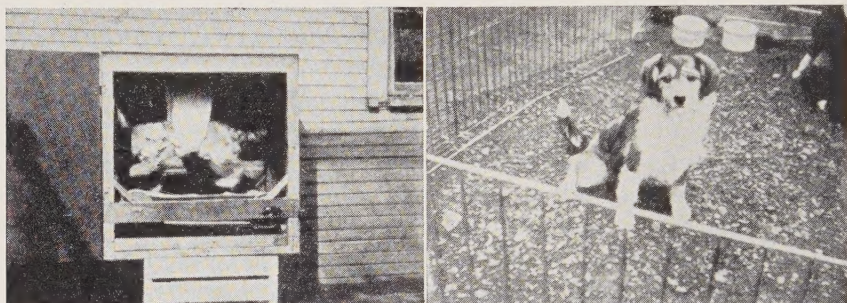


FIG. 1. Animal 3b. Slings under the hind legs were added later

FIG. 2. Animal 1b, 6 months old

ever the closeness of the side walls and the sling prevented the animal from elevating his leg. Each of the two delayed dogs was placed in the apparatus before his male littermates had elevated the leg when urinating, and was kept there until several weeks after the male littermate controls were regularly elevating the leg when urinating.

TABLE I
THE EXPERIMENTAL PLAN

Litter	Animal	Treatment
1. Secured when 12 weeks old	a. male b. female	control conditioning
2. Secured when 4 weeks old	a. male b. male c. female	control * castrated control
3. Secured when 5 weeks old	a. male b. male c. male d. male e. female	castrated delayed * control * control male sex hormone
4. Born under laboratory control	a. male b. male c. male d. male e. female f. female	castrated anosmic control delayed control male sex hormone
5. Born under laboratory control	a. male b. male c. male d. male e. male	male sex hormone anosmic anosmic control control
6. Secured when about 10 years old	a. female	male sex hormone

* After these animals had served as controls, they were used to study the effect of female sex hormone injections.

Castration of three animals was accomplished by complete removal of both testicles.³ Of the dogs rendered anosmic, the nerve endings of the nasal fissure were coagulated in one animal, and the olfactory bulbs were removed in two other animals.

Because very old or ovariectomized female dogs are sometimes known to elevate the leg when urinating, it was planned to use male sex hormones in an attempt to produce similar leg-elevation behavior in females. Also, it was planned to attempt to produce female leg-raising by means of conditioning. Injections of male sex hormones were given to castrated animals and to very young puppies, and the effects of such treatment observed. Female sex hormones⁴ were administered to normal adult male dogs in an attempt to disrupt the adult leg elevation behavior.

RESULTS

The urination pattern in puppies.—In very young male and female puppies, i.e., those less than two weeks old, there is no urination posture. They urinate while creeping, while lying on the side, or while nursing. About once every hour or hour and one half, a small quantity of urine is released. The release of urine is in the form of

TABLE II
AVERAGE NUMBER OF ACTS OF URINATION PER TWO-HOUR OBSERVATION PERIOD *

Age in Weeks	Females (Normal)	Males (Normal)
0-4	1.1	1.2
5-8	1.0	1.4
9-12	0.6	0.9
15-16	0.8	3.4
17-20	1.3	8.3
21-24	1.1	11.7
25-28	1.1	9.8
29-32	1.0	12.4

* The total number of observation periods was 103. The total number of acts of urination observed was 2317. Four to six females and 10 to 16 males were observed in securing the data. The number of animals varied for observation periods because of experimental conditions. Records were not included for experimental animals.

a trickle, suggesting that when a certain fullness of the bladder occurred the sphincter relaxed. At this stage, the bladder-emptying appears to be mechanically controlled rather than under nervous control.

Between the ages of three to five weeks, a differentiation in the urination posture appeared between the male and female puppies of the group studied. All female dogs squatted on the hind legs in a characteristic posture when urinating (Fig. 2). This posture is quite similar to the defecation posture of both males and females. The male puppies, on the other hand, stood when urinating. The

³ The author wishes to express his thanks to Dr. Vincent Rees and to Mr. William Troy of the University of Michigan Department of Surgery for performing the operations required in this study.

⁴ The author is indebted to Dr. Oliver Kamm of Parke, Davis and Company and to Dr. Erwin Schwenk of Schering Corporation for supplies of sex hormones manufactured by their respective firms. Without their friendly cooperation this investigation would have been greatly handicapped.

hindquarters of the younger puppies were observed to be held relatively lower, in a semi-squatting position. As male puppies matured they stood relatively more erect (Fig. 3). This last was only a tendency; that is, some male puppies of the groups observed rarely squatted very low when urinating. At no time did a normal



FIG. 3. Animal 3b, 7 weeks old

FIG. 4. Animal 5c. Locomotion when 7 days old

puppy in any of the groups studied elevate the leg when urinating before the age of 19 weeks.

With increasing age, the male puppies urinated less copiously but more frequently than the females. During a two-hour observation period, each female usually urinated once, although occasionally a female urinated twice or not at all. The female puppies urinated copiously, apparently emptying the bladder in one act of urination. Up to the age of 12 weeks the same was true of the male puppies. After the age of 12 weeks the males urinated more frequently and 'sniffed' the ground more often, although they did not elevate the leg when urinating until some weeks later.

Locomotion in the very young puppy is accomplished mainly with

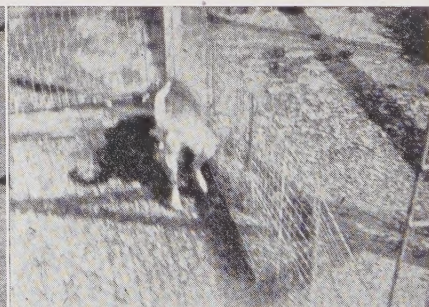


FIG. 5. Animal 5e, 27 days old

FIG. 6. Animal 5e. Initial stage of leg-elevation at 23 weeks

TABLE III
AGE OF FIRST APPEARANCE OF LEG-ELEVATION

Animal.	1a	2a	3b*	3c	3d	4c	5d	5e	Mean
Age in Weeks.....	43	36	24	19	20	35	24	23	28.0

* This animal was delayed in a sling; hence the true age of the appearance of leg-elevation behavior may have been about 20 or 21 weeks.

the forepaws, the hindquarters dragging or moving in a manner uncoordinated with forequarter action (Fig. 4). The direction of locomotor development appears to be clearly caphalo-caudal. When two or three weeks old the animals walked erect, but not in the digitograde mode of progression characteristic of the adult dog. Instead, the entire plantar surface of the hind leg was in contact with the ground, much like the hind leg of a rabbit (Fig. 5). In the group of animals studied, no urination posture was noted in males or females until after the animals walked erect in a fairly well-coordinated manner. Also, no male elevated the leg when urinating until

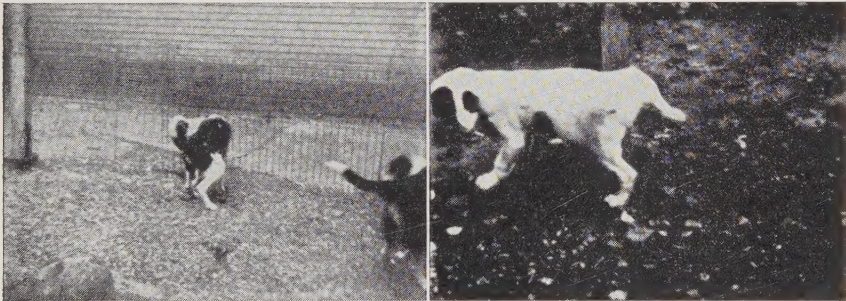


FIG. 7. Animal 2a. Torsion movement of back during urination—age 36 weeks

FIG. 8. Animal 5a. Leg not crooked—age 9 weeks

some weeks after the assumption of a digitograde position during walking. It should be noted that two-week-old pups were observed to *rise* to a digitograde position, but they were not observed to walk or run in this position.

The adult male urination pattern.—Several stages in the development of leg-elevation behavior were found. Initially, there was a gross torsion movement of the hindquarters in which large muscle groups were brought into action and the leg was lifted one or two in. from the ground (Fig. 6). Occasionally, the leg remained touching the ground although the torsion movement was clearly present (Fig. 7). The next stage was a higher leg-elevation in which the leg was moved outward from a point of articulation at the hip without

the leg's being crooked or drawn in close to the body (Figs. 8, 14). The third stage consisted in the bending or crooking the center of the leg and drawing it close to the body (Fig. 9). The only changes with increasing age noted in the behavior sequence after this third stage were a higher elevation of the leg (Fig. 10) and, in two animals, a more complete individuation of the leg-elevation pattern so that the toes of the paw were splayed.

Thus, the leg-elevation pattern was found to consist of stages in which activity progressed from the hindquarters to the hip, from the hip to the center of the leg, and in two cases to the toes of the paw. The emergence of this pattern was strongly suggestive of a proximo-distal direction of development.

The leg-elevation pattern required two to three weeks to develop from the initial torsion movement of the hindquarters during urina-

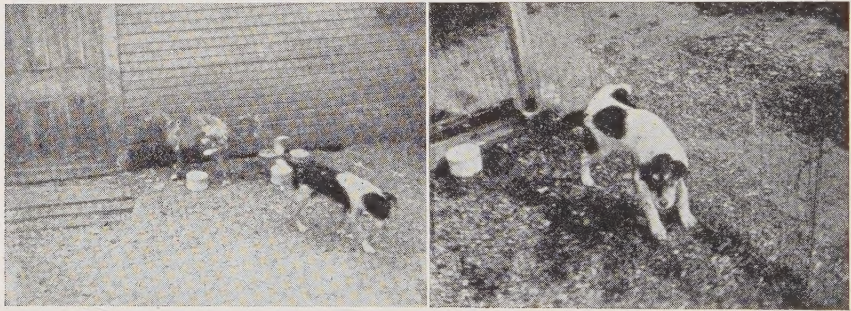


FIG. 9. Animal 3b. Urination in open—age 26 weeks

FIG. 10. Animal 3c. Adult urination posture—age 27 weeks

tion to the complete act of leg-flexion articulated at the hip. During this early period of leg-elevation, the animals frequently urinated in the open—that is, urinated without directing the stream against an object as a wall or a post. Also, some animals would approach a wall and then urinate away from the wall (Fig. 9).

Regression to puppy urination posture.—Adult male dogs that had been regularly elevating the leg when urinating were observed to revert to the puppy posture after being exposed to what may be called fear-arousing situations. This was first noticed in an adult male that had been observed to elevate the leg 231 times without assuming the puppy posture. This dog was placed in the exercise yard for observation when a tree which workmen had been felling nearby crashed to the earth. The dog yelped and cringed. The animal then crawled to the experimenter, its hind feet in a plantigrade position. Shortly afterward, the animal urinated, assuming the

puppy stance. The following day the leg was elevated in the normal adult manner.

Five males that had elevated the leg when urinating 100 or more times were subjected to stimuli such as a smart slap on the nose, an electric shock from a Ford spark coil, and a loud noise obtained by bursting inflated paper bags near the animal's head. In a total of 29 trials with such stimuli the dogs regressed to the puppy posture in 28 cases. The single exception occurred when a paper bag was burst and the noise did not appear to be as loud as was found in later trials with other paper bags.

Control of practice in leg-elevation.—Practice was controlled by placing the animal in a treadmill cage (Fig. 1) designed to control leg-elevation. Animals 3b and 4d were placed in the apparatus during different periods; however, animal 4d contracted distemper and died before his delay period was complete. Thus, only the results of dog 3b are available.

Animal 3b was strapped in the delay apparatus when 15 weeks old. Neither this animal nor any of his normal littermates elevated the leg at this age. The animal was not removed from the delay cage until the end of the delay period; feeding and cage cleaning were done while the animal was in the delay harness. The dog appeared to adjust well to the delay condition in about a week's time. When 19 weeks old, this animal's littermate, 3c, showed the leg-elevation pattern when urinating. A week later, littermate 3d also revealed the pattern. Although the delay animal was observed daily when urinating, he made no attempt to elevate the leg when urinating. The slings and narrow cage would, of course, have prevented complete leg-raising; however, it is stressed that the animal was not observed to make even a partial leg-flexion. The dog was kept continuously in the delay apparatus for a total of nine weeks until almost 24 weeks old. At this age his control littermates 3c and 3d had been raising the leg when urinating for five and four weeks respectively.

At the end of the delay period, the animal was fed and given milk before being removed from the cage and placed in the exercise yard. When placed outdoors, the animal cowered on the ground and crept after the experimenter. The animal did not urinate or make any attempt to explore the exercise pen. The dog was then returned to the cage, and shortly afterward he urinated copiously. On the second day, food and milk were placed in the yard, but the animal refused to eat and did not urinate outdoors. On the third day, a female littermate was placed outside with the delay animal and a large quantity of meat and milk were placed in the yard. The female ate readily; the delay animal ate more hesitantly. In five hours each animal urinated once. The male assumed a puppy

urination stance. After being removed from the delay cage on the fourth day, the animal did not cringe when placed outside. He ate readily and drank a large amount of milk. About a half-hour afterward he urinated, raising the leg completely. It was a complete, individuated leg-elevation. The animal did not direct the urine stream against an object but urinated in the open (Fig. 9). He continued to elevate the leg regularly, although for several weeks he did not urinate on objects such as a post or wall.

Another control over practice was instituted in a less complete manner. Animal 5e was placed alone in a cage when six weeks old. He was not allowed to exercise in the yard. Also, his cage was so placed that he could not see other animals. Thus, there was no opportunity to learn by imitation, nor was the olfactory stimulus of urine from other animals immediately available except for such odors as might come from a distance of 20 feet. Trial and error learning, of course, was possible. Under these conditions the animal elevated his leg when 23 weeks old, the first of his litter to do so.

Results of castration.—Three males of different litters, animals 2b, 3a, and 4a, were castrated by complete removal of both testicles when 11, 7, and 4 weeks old respectively. Animal 4a died five days after the operation, apparently as a result of post-operative infection. The remaining dogs were observed on alternate days. Both animals continued to assume the puppy urination stance for several months after their control littermates had been regularly raising the leg when urinating.

When 41 weeks old, dog 2b had not been observed to make any attempt to raise his leg during urination, although his control littermate had been elevating the leg for five weeks. At this time 25 mg. of testosterone propionate in one cc. of sesame oil was injected intramuscularly in the buttock on alternate days for four days, a total of 100 mg. testosterone propionate. On the ninth day after the initial injection the animal raised his leg completely when urinating. No further injections were given, and on the sixteenth day the dog reverted to the puppy urination posture. No further changes in posture were noted thereafter. On the twenty-fifth day after the first injection the animal became ill with what was apparently distemper. Although treated with sulfapyridine as suggested by Troy (37) the animal died two weeks later.

Castrated animal 3a continued to reveal the puppy urination stance up to the age of 33 weeks, although his control littermates had been elevating the leg during urination for 10 or more weeks. This castrated animal was given 25 mg. of testosterone propionate in one cc. sesame oil injected in the buttocks on alternate days. After the third injection it was observed that the frequency of urination

increased from two to three times in a $1\frac{1}{2}$ hour observation period to seven to nine times, although the leg was not elevated. After six injections of testosterone, 13 days after the initial injection, the animal elevated his leg completely when urinating. The leg-elevation was completely individuated, including a crooking of the leg (Fig. 11).

The animal continued elevating the leg for six days after the last injection of testosterone. On the seventh day and for four days

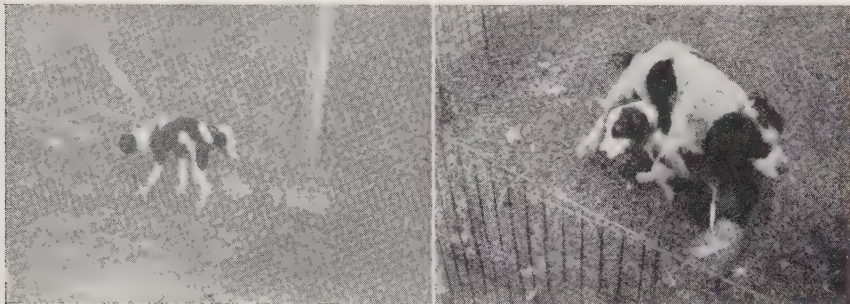


FIG. 11. Animal 3a (castrate). Urination posture after testosterone treatment—age, 32 weeks
FIG. 12. Female 6a mounting female 4c after testosterone treatment

afterward the animal reverted to the puppy posture when urinating. Frequency of acts of urination also decreased. Then, one 25 mg. injection of testosterone was administered on the eleventh day after the last injection. This was the seventh 25 mg. unit administered. On the day following, the animal urinated four times in a $1\frac{1}{2}$ hour period, elevating the leg once and assuming the puppy posture three times. Thereafter, no reversion to the puppy posture occurred until the fourth day after the last hormone injection. Of two acts of urination on the fourth day, one was in the puppy posture. On succeeding days the puppy posture was employed exclusively. No testosterone was administered for 22 days after the seventh injection. Beginning with the 23rd day, injections 8, 9, and 10 of 25 mg. of testosterone each were administered on alternate days. The puppy urination stance was observed to persist until the day after injection 10. The animal continued to elevate the leg when urinating for five days after injection 10 without additional hormone treatment. After the fifth day, a reversion to the puppy stance was observed which continued until injection 11.

Injection 11 was also 25 mg. testosterone. This injection was administered nine days after injection 10. On the day following injection 11, the animal elevated the leg completely and continued to do so for five days. On the fifth day, the animal returned to the

puppy urination posture. The animal was observed daily for two weeks after the return to the puppy which followed injection 11 and on alternate days for six additional weeks, but no leg-elevation during urination was observed. During the last four weeks of this period, the animal was allowed to remain all day in the exercise yard with a normal adult male, in order to check for the possible influence of imitation. No postural change occurred in either animal. The castrated animal continued to assume the puppy stance during urination.

Estrogen administration to adult male dogs.—Since leg-elevation in castrated male dogs appeared to relate to the presence of a male sex hormone, it was planned to attempt to break the leg-elevation pattern in normal adult males by the injection of female sex hormones. After animal 3b had completed the delay period and after animals 3c and 2a (controls) had been elevating the leg during urination for several months, they were treated with theelin and estradiol benzoate, female sex hormones. Animals 3b and 2a were injected with theelin, animal 3c with estradiol benzoate. Because nothing in the literature suggested an optimal dose for studying the effects of estrogens upon the behavior of dogs, large doses were employed at first.

The first animal thus treated was 3c. This animal was given 10,000 I.U. estradiol benzoate each day for eight consecutive days. Half of the dose was injected in each buttock. The results of this treatment were striking. The leg-elevation pattern was not broken, but rather reinforced. The animal urinated with increasing frequency, elevating the leg each time. After the first six or seven leg-elevations no further urine was expelled; however the animal continued to sniff about walls and posts and briefly elevate the leg.

The animal's behavior might best be described as *frantic*. He literally spent all of his time in darting about the exercise yard, pausing briefly to elevate the leg for one or two seconds. Urine was expelled during the first six or seven acts of leg-elevation. These first leg-elevations were of longer duration. No urine was expelled afterward, although leg-elevation continued, sometimes as often as 70 times in a half hour (Table III). The animal appeared to be oblivious to stimuli which previously had had marked attention value. Formerly, the passing of a freight train nearby would cause the animal to prick up his ears and then bark. The animal also had played with a stick or an old rag quite frequently when in the exercise yard. None of this earlier behavior was observed during the period of 'frantic urination.' The animal appeared concerned only with darting about the yard, sniffing, and raising the leg. When allowed in the yard for several hours, the animal eventually fell asleep. Also, the animal appeared to sleep much more than the other dogs

TABLE III
LEG-ELEVATION OF ANIMAL 3c AFTER ESTROGEN TREATMENT

Day	Number of Leg-Elevations	Period of Observation (Min.)	Average No. Elevations Per Min.
*4	14	20	.70
*5	27	33	.82
*6	32	35	.91
*7	76	30	2.53
*8	72	31	2.32
9	139	64	2.17
10	61	28	2.18
11	11	67	.16
12	15	41	.36
16	3	22	.14
23	3	36	.08

* On these days and on the three days preceding, 10,000 I.U. estradiol benzoate were administered.

when confined in the cage. Animals 3b and 2a manifested the same pattern with similarly large injections of theelin.

These results were discussed with Professor A. E. Woodward of the University of Michigan Zoölogy Department. She suggested using smaller doses of estrogens. Accordingly, animal 3c was given 1000 I.U. estradiol benzoate on alternate days for 11 days. Animals 2a and 3b were given 2000 I.U. theelin on alternate days for 11 days. Each animal had a total of six injections. The hormones were administered four weeks after the end of the previous series of 10,000 I.U. daily.

Animal 3c reverted to the puppy posture on the day following the sixth injection, the twelfth day of the injection series. Animal 3b ceased elevating the leg during urination on the ninth day, the day of the fifth injection. Animal 2a became ill with distemper before the sixth injection of female sex hormones was administered. While this animal did employ the puppy urination posture, the disease may have influenced this pattern. It is known that distemper can result in chorea and similar nervous disorders (see Cannon, II, p. 16).

Administration of androgens to female dogs.—Dog owners sometimes report that old female dogs occasionally elevate the leg when urinating. Two females that manifested such behavior were observed by the experimenter, although they were not used in this experiment. One animal was a 15-year-old mongrel that had borne many litters; the other was a six-year-old spayed Boston terrier owned by Professor Willard C. Olson. Since one animal was past the litter-bearing state and since the other was ovariectomized, it was believed that a hormonal imbalance might relate to the leg-raising behavior. It was planned to attempt to secure similar leg-elevation behavior in females by the injection of testosterone propionate.

Two animals were used, animal 6a, about 10 years old, and animal 3e, 14 weeks old. Animal 6a had borne several litters, and animal 3e had never been in estrus.

Three periods of androgen administration were used with animal 6a. No hormones were given for 12 days between each period. During the first period, female 6a was given an injection of 25 mg. testosterone three times a week for three weeks, a total 10 injections, or 250 mg. testosterone. No change in urination posture was observed. There was a slight increase in frequency of urination during the last week of this period. In the second period an injection of 25 mg. testosterone was given daily for 10 days, a total of 250 mg. No change in posture was observed. The animal urinated an average of three times per two-hour observation period, which was about three times the normal frequency listed in Table II. During the third period, 37.5 mg. testosterone was injected daily for eight days, a total of 300 mg. The female urination posture remained unchanged. The frequency of urination was the same as the second period, or about three times the average for normal females. Thus, after a total of 800 mg. testosterone propionate was injected, no change in urination posture was found.

Animal 5e was given 16 injections of 25 mg. testosterone on alternate days, a total of 400 mg. No change in the urination posture was observed. The frequency of urination increased after the third injection from once to an average of two and one-half times during a two-hour period.

Although no changes in urination posture were observed in either animal, both females did reveal the male copulatory pattern. After the fifth 25 mg. injection, animal 6a mounted a young female. Animal 3e revealed similar behavior after the fifth injection. The mounting behavior was not always directed at the hindquarters of the mounted animal but frequently the head was mounted (Fig. 12). A male was let out in the exercise yard with animal 6a. Although the male struggled, he was firmly clasped and the female executed a series of rapid piston movements. With increasing doses of the male sex hormone, both animals more frequently mounted other males or females placed outside with them. Female 6a particularly was observed to mount other animals almost continuously during the two-hour observation period. Her mounting behavior was similar to the 'frantic' leg-elevation behavior of animals 3b and 3c. She would mount an animal, would be shaken off, and would immediately mount the animal again. Three weeks after the injections were discontinued she no longer revealed this copulatory behavior. Animal 3e ceased exhibiting the male copulatory pattern nine days after the last injection.

Androgens administered to an immature male dog.—Previous studies have demonstrated that testosterone administered to very young male rats or male chicks results in a premature appearance of the copulatory pattern. It was planned to treat a young puppy in a similar manner to observe the effect upon leg-elevation. When six weeks old, animal 5a was given $12\frac{1}{2}$ mg. testosterone daily for 14 days. Because of the numerous observations being made of other animals, this animal was not observed until the day of the fourteenth injection when he was eight weeks old. On this day, the animal elevated the leg four times when urinating in a 35-minute period.⁵ The leg-elevation was completely individuated, including crooking of the leg (Fig. 13). It is probable that the pattern appeared before



FIG. 13. Animal 5a. Leg-elevation at age 8 weeks. Treated with testosterone

FIG. 14. Animal 5a. Age 10 weeks. Treated with testosterone

this time but was not observed. The littermates of this animal did not elevate their legs when urinating until several months later, littermate 5d at 24 weeks and 5e at 23 weeks.

No testosterone was administered for two weeks after the close of the 14-day hormone injection period. It was observed that six days after the last hormone injection animal 5a revealed a less individuated urination posture in that the leg was not crooked (Fig. 8). Three days after this, nine days after the last injection, a reversion to the puppy posture occurred. When the animal was 10 weeks old, five mg. testosterone was injected in the buttocks daily for three days. On the day of the third injection, an incompletely individuated leg-elevation occurred during an act of urination. During a second act of urination, the puppy position was assumed. On the day following, a completely individuated leg-elevation was observed. This behavior continued without reversion to the puppy stance for 15 days. On the sixteenth and seventeenth days after the

⁵ It is interesting to note that the testes of this animal had descended and were easily palpated at this time.

last injection a partially individuated leg-elevation was noted. Thereafter the puppy stance was employed without exception during urination for almost two months. When 20 weeks old, the animal began to elevate the leg regularly although no testosterone had been administered for more than nine weeks.

Attempted control of olfaction.—An attempt was made to render animal 4b anosmic by coagulating the nerve endings of the nasal fissure. The original plan called for excision of the olfactory bulbs; however, because of the thickness of the skull and danger to the eyes, this plan was abandoned. It was thought that the thinner and softer skull of puppies might make this operation less hazardous. When six days old, animal 5b was subjected to successful olfactory bulb excision, but the animal died about an hour later. Animal 5c was similarly operated on when 18 days old. This animal died three days later. The attempt to render animal 4b anosmic by coagulation of the nasal fissure nerve endings was likewise unsuccessful. Simple tests made with meat placed under inverted pans indicated that this animal could respond to olfactory stimuli.

Since surgical techniques were unsuccessful, an attempt to control olfaction was made by inserting a pellet of cotton dipped in oil of wormseed in the nostrils of animal 5d when he was 17 weeks old. The nostrils were carefully swabbed with petroleum jelly daily and a fresh cotton pellet was inserted. The animal adjusted to this condition and ate food readily after a week's time. This animal was observed on alternate days when 18 weeks old. He was placed in a small concrete floored pen several hours after the floor of the pen had been washed with a lysol and soap solution. Under these conditions the animal began to elevate the leg when urinating when 24 weeks old, a week later than his control littermate 5e. The only change noted in his behavior was that he did not sniff the ground as normal animals do. The animal did urinate on posts as if visual stimuli were related to this behavior.

Leg preference of adult male dogs during urination.—It was observed that animal 3d raised only the right leg when urinating. If he

TABLE IV
LEG PREFERENCE DURING URINATION

Male	No. Right-Leg-Elevations	No. Left-Leg-Elevations	Total
1a	51	69	120
2a	97	62	159
3b	88	51	139
3c	93	40	133
3d	247	0	247
Total	576	222	798

approached a wall or post from his left, he would raise the right leg and urinate away from the object. This was during the first few weeks of leg-elevation activity. Later, if he approached a wall from his left, he would turn around before raising the right leg so that the wall was now on the right. A record was kept for five weeks of the leg elevated by animals 1a, 2a, 3b, 3c, and 3d. These data are summarized in Table IV. It seems clear that some male dogs may exhibit a leg preference for acts of urination.

DISCUSSION

Dog owners and kennel operators often refer to a male dog's 'learning to lift the leg' as if the process were of a trial and error nature. Yet, mere observation of a pattern of behavior gives no clue as to whether learning or maturation is responsible, as Maier and Schnierla (22, p. 374) remark. Two lines of evidence in this study oppose a trial and error interpretation of leg-elevation behavior in male dogs. First, there is the evidence of a cephalo-caudal direction of development which was followed by a proximo-distal direction of leg elevation behavior. The second line of evidence in this study concerns the results of castration, delay, and androgen administration to young puppies. That is, castrated animals should have 'learned' to lift the leg when urinating, but they did not. An animal delayed in a sling without opportunity to practice should have exhibited random, trial and error movements instead of a complete leg-elevation after being released from the delay cage. Also, male sex hormones administered to a young puppy should not have resulted in leg-elevation behavior at eight weeks and 'forgetting' of the pattern at nine weeks when hormone injections ceased.

Thus, maturation appears to be responsible for leg-elevation behavior in male dogs. This behavior is universal among normal adult males, and it is sufficiently complex to be designated as *instinctive*. What appears to be learned in canine micturition behavior is the directing of the urine streams against an object such as a wall or post. During the early stages of the appearance of the pattern, it was noted that several animals frequently urinated in the open or away from an object. Older males rarely did this.

The age at which leg-elevation first occurred during urination may have been affected by temporary dietary deficiencies in the case of litters 1 and 2. While dog owners report ages as high as 11 months for the appearance of leg-elevation behavior, it is possible that dietary deficiencies may cause a delay in the appearance of this pattern in such cases also. Allen (1, p. 1173) states that vitamin B deprivation is known to result in atrophy of the sex organs and

reduced testicular hormone output. Stone (32) found that qualitative inanition caused a delay in the appearance of copulatory activity in white rats. Since a testicular hormone was shown to relate to leg-elevation in males and since a vitamin B₁ deficiency was found to exist temporarily in the diet of litters one and two, it is possible that a delay in the appearance of this pattern may have occurred in some cases.

Milk was omitted from the diet of all animals at age 15 weeks. The two oldest groups, the animals of litters 1 and 2 began to refuse food, becoming extremely timorous at the approach of the experimenter, shortly after the exclusion of milk from the diet. Some animals had several convulsive seizures, and animal 1a exhibited a paralysis of the hindquarters. The symptoms and course of this disorder were quite like those of 'fright disease' as described by Patton (25). Patton pointed out that thiamin chloride, vitamin B₁, was heat labile and thus destroyed by autoclaving. He emphasized that animals fed exclusively on prepared dog's foods were receiving a diet deficient in B₁ unless this vitamin were later added, because the high temperatures destroyed the vitamin. In accordance with his suggestions 600 I.U. thiamin chloride in sterile distilled water was injected subcutaneously.

The effect of the B₁ injections was striking. Within six hours after the first injection all animals drank a small amount of beef broth which had previously been ignored. The paralysis of animal 1a disappeared within eight hours. Similar injections were given for three more days. By the fourth day the animals appeared to be quite normal. Thereafter, raw beef and milk were fed daily, since these foods contain adequate amounts of B₁. The prepared dog foods were eliminated from the diet. No further evidence of avitaminosis was noted during the remainder of the experimental period.

The results of the castration experiments are considered to be sufficiently well delineated to permit a direct interpretation. It is known that androgens appear in quantity at the time of puberty in normal males (see Best and Taylor, 9, p. 1196f.). Studies already cited have demonstrated that male copulatory behavior is normally absent in castrated adult rats; however, when such animals were treated with sex hormones the copulatory pattern was restored. The failure of castrated males in this study to reveal the adult male leg elevation behavior is considered to be similar to the absence of copulatory activity in castrated male animals reported in other studies.

The action of the male sex hormone used in the castration experiments appears to be an activating or energizing of an existing but hitherto inactive neural or neuromuscular organization. It cannot

be assumed that the action of the hormone is to produce nerve growth and thus form the necessary sensori-motor connections, since if this were the case there should be no reversion to the puppy stance after hormone injections were halted. It will be recalled that the leg-elevation pattern was made to appear and disappear four times in castrated animal 3a. Further evidence that arrested nerve development is not a likely explanation for these results is found in the work of Kudanoff (19), who observed that nerve endings in the genital area of mice castrated shortly after birth continued their development. Other evidence which will be presented later indicates that the neural organization concerned with this behavior is probably matured at birth or shortly afterward.

The results of androgen administration to females permit several interpretations. Since the attempts to produce this pattern by means of hormone injections were unsuccessful, it may be that some explanation other than hormonal may account for the leg-elevation of an occasional female, such as the animal belonging to Professor Olson. It is possible that while maturation is responsible for leg-elevation in the male, trial and error learning or conditioning might relate to similar behavior in an occasional female. But the two females that were observed to elevate the leg during urination did so only half the time or less. Trial and error learning would suggest more regularity in the appearance of such behavior. Also, it should be expected that more variation would be observed in the female urination posture, instead of either a squatting posture or a complete hind-leg-elevation. The same arguments may be advanced against conditioning. An attempt was made to condition female 1b by administering an electric shock whenever an attempt to squat and urinate was made. No change in posture occurred even after she was shocked 39 times. A final significant point is that the two leg-elevating females observed, and similar females described by dog owners, are either ovariectomized or relatively old, suggesting an altered hormone condition.

Allen (1, p. 588) refers to endocrine intergrades. Some animals of various species are as much male as female from an endocrine standpoint, regardless of the appearance of the external genitalia. Such animals may show copulatory activity ordinarily associated with either or both sexes. Conceivably, such endocrine intergrades might explain the male leg-elevation behavior of certain females.

A third possible explanation is suggested by the work of Ball and of Beach. Ball (5, p. 164) concluded that ". . . the male copulatory pattern in more or less rudimentary form is part of the equipment of the normal female rat. The threshold of this behavior pattern is very high normally but it can be lowered by testosterone administration.

. . .” Beach (8) found that some *untreated* female rats revealed a complete male copulatory pattern. Stone (31) noted that some untreated male rats occasionally exhibit portions of the female copulation pattern. Such findings, as Beach states (8, p. 141), “. . . suggest that some individuals may inherit or acquire the neural organization mediating the mating pattern of the opposite sex.”

These studies, while referring to copulatory behavior, may relate to the failure to secure female leg-elevation during urination. That is, the threshold may not have been lowered sufficiently to activate the male leg-elevation pattern, or these particular animals may have lacked the appropriate neural organization necessary for this pattern. Other female animals that do reveal the leg-elevation pattern would on this basis be said to possess the appropriate neural organization. Similarly, it might be assumed from this viewpoint that the threshold might have been lowered sufficiently to cause leg-elevation if testosterone had been administered for a longer period of time. It is possible that more conclusive results might be obtained by using ovariectomized animals in a similar study.

The administration of female sex hormones to normal males produced complications worthy of elaboration. The leg-elevation during adult male urination was ultimately disrupted and a reversion to the puppy urination posture occurred after treatment with estrogens. This suggests, as do the castration results, that the leg-elevation pattern is hormonally controlled. Morrell and Hart (23) found that testicular function was eventually suppressed by administration of estrogens such as stilbestrol. This would suggest that the prolonged administration of female sex hormones to the dogs used in this study may have suppressed testicular activity, resulting in lesser testosterone secretion and a reversion to the puppy urination posture. The cessation of the female sex hormone injections would then permit a gradual restoration of testicular function to an approximately normal level and, hence, a resumption of normal adult male leg-elevation behavior.

But the ‘frantic’ leg-elevation behavior which occurred when large (10,000 I.U.) injections of female sex hormones were administered is frankly puzzling. It will be recalled that treated males sometimes elevated the leg as often as 100 or more times in an hour, although no urine was expelled after the first seven or eight leg elevations, and then fell asleep. Dr. Gardner Riley of the University of Michigan Hospital has noted that large doses of estrogens appear to promote the formation of calci in the bladders of rats. Hence, it was at first thought that the frantic leg-raising might be the result of bladder irritation due to calci. But this explanation is inadequate, since it was later found that the frequency of leg-elevation dropped

with the cessation of estrogen administration. Calci in the bladder should be expected to provide a more constant irritation.

The results of Ball (3) suggest what appears to be a more tenable explanation. She found that administration of female sex hormones to castrated male rats resulted in an increase in sex activity in four of six animals. She suggested that gonadal hormones activate a mating pattern which is already present. It is possible that the existing and functioning leg-elevation patterns in the adult males used in this study were more strongly or more frequently activated by the estrogen treatment. Thus, while large amounts of female sex hormones were adequate to energize the leg-elevation pattern, small amounts were not. The use of small amounts of the hormone might be interpreted as being inadequate to cross or lower a threshold of the type described by Ball (3). Then, if testicular function had been suppressed as previously suggested, a reversion to the puppy urination stance would occur.

The leg-elevation behavior noted in an eight-weeks-old puppy treated with testosterone is analogous to the precocity in copulation described in studies by Stone and Noble and Zitrin which have already been cited. This behavior appeared two months earlier in the treated animal than in the control littermates. Such behavior might be explained as being due to increased neural growth resulting from the hormone treatment. But this is not likely; for if the action of testosterone were merely to hasten nerve development, then once this development had occurred the necessary connections should have been made and there should be no reversion to the puppy urination posture. The experimental animal did, however, return to the puppy position when testosterone was no longer administered.

It might, of course, be assumed that testosterone speeded nerve development and then activated the matured sensori-motor organization. On this basis, the reversion to the puppy stance occurred because the hormone activator was no longer present although the neural organization was mature. Such an interpretation is possible. However, as already discussed, other studies indicate that the neural organization of the mating pattern is complete at birth or shortly afterward. It is believed likely that the sensori-motor basis for the leg-elevation pattern in male dogs is similarly present at birth or shortly thereafter, since no studies of similar behavior indicate that under similar conditions testosterone promotes nerve growth.

A hypothesis concerning individuation in canine leg elevation.—If it is assumed, as it is in this paper, that the nervous organization mediating leg-elevation behavior during urination of adult male dogs is complete shortly after birth, it is necessary to explain how individuation in such leg-elevation behavior can occur. The increasing

specificity of sensori-motor connections described in the work of Coghill (13) would not apply where the sensori-motor organization is complete. It is believed that an explanation based upon hormonal activity can be advanced which will fit the facts presented in this study.

The problem of just what the nature of hormonal action is has been a knotty and much discussed one. In a review article, Lashley (21) examines and evaluates the evidence bearing upon this problem. He asks (p. 459), "Does the hormone stimulate the growth or formation of new nervous connections . . .?" and concluded, from evidence similar to that presented in this paper, that neural connections are already laid down and the hormone is only an activator. He then raises the question (p. 460), "Does the hormone act merely by increasing the general excitability of the organism?" and concludes that hormones act too specifically as shown by cases of sex reversal, etc., for this to be true. He points out that hormones are not likely to act by causing specific changes in organs as testes, vaginal mucosa, mammae, etc., because removal of the reproductive system results in normal sexual responses when hormones are administered. Lashley then comments (p. 462), "There remains only the last alternative, that the hormones act upon the central nervous system to increase the excitability of the sensori-motor mechanisms specifically involved in the instinctive activity." He considers this last interpretation to be plausible. Seward (26) also believes the evidence points to direct hormonal action upon the central nervous system.

Two general conclusions are found in the studies cited in this paper and the studies evaluated by Lashley. (1) Hormones act upon established nervous organization, and (2) there exists a threshold for the activation of an instinctive pattern which relates to the amount of hormone present. The proposed interpretation would assume that different thresholds exist requiring varying amounts of a given hormone, for exciting portions of the sensori-motor mechanism controlling leg-elevation behavior. Large amounts of testosterone, for example, would thus activate the entire leg-elevation pattern, while lesser amounts would activate only a part of it. This may be summarized as follows:

X amount of testosterone crosses threshold I, activating the sensori-motor mechanism responsible for the gross torsion movement of the first stage of leg-elevation; X + Y amount of testosterone crosses thresholds I and II, activating the sensori-motor mechanisms which produce both torsion movement and leg-elevation articulated at the hip; X + Y + Z amount of testosterone crosses thresholds I, II, and III, producing the torsion movement, leg-elevation articulated at the hip, and crooking of the leg.

The fact that a maturing male dog secretes gradually increasing amounts of male sex hormones would fit in with this hypothesis. That is, as the animal matured, sufficient testosterone would be produced to activate sensori-motor mechanism I, producing the torsion movement of the back. Larger amounts of testosterone secreted later would progressively cross other thresholds and activate other mechanisms, producing more specific behavior. This hypothesis would likewise explain why lesser amounts of testosterone produced only a partially individuated leg-elevation in animal 5a. It would also explain why castrated animal 3a was observed to revert from a complete leg elevation to a partially individuated leg-elevation and then to the puppy posture after testosterone injections were halted.

SUMMARY AND CONCLUSIONS

The micturition behavior of 22 dogs, 16 males and six females, was studied under various experimental conditions. Littermate controls were employed in determining the effect of castration, control of practice by delay in a sling and treadmill apparatus, injection of male or female sex hormones in experimental animals, and control of olfaction. Direct observation and motion pictures were used in recording the results of these experimental conditions, as well as the development of the normal micturition pattern.

It was found that there was little distinction in the urination posture of young male or female puppies, both sexes employing a squatting position. With increasing age, males tended to stand more erect when urinating and also to urinate more frequently but less copiously than females. Normal females did not at anytime elevate the leg during urination. Normal males elevated the leg when urinating as early as 19 weeks of age and as late as 43 weeks in the group studied.

It was found that development of locomotion followed a cephalo-caudal direction. Leg-elevation behavior in males was not observed until several months after locomotor development was relatively complete and the animals walked in a digitgrade manner. The development of leg-elevation was found to be sequential and to follow a proximo-distal direction. Three main stages in leg-elevation were observed: a gross torsion movement in which the leg was elevated only an inch or two from the ground; a higher leg-elevation articulated at the hip in which the leg was straight, a complete leg-elevation articulated at the hip which included a crooking of the leg. In some animals a further individuation was noted in the splaying of the toes of the paw.

It was observed that normal adult male dogs regressed to the puppy posture of urination when subjected to what appeared to be fear-arousing stimuli. Practice in leg-elevation was controlled by placing a young puppy in a sling and treadmill apparatus which prevented leg-elevation. Although confined continuously in this apparatus for four weeks before and five weeks after his control littermates exhibited leg-elevation behavior, this 'delayed' animal revealed a completely individuated leg-elevation posture shortly after being released from the delay cage. Castrated animals did not reveal leg-elevation behavior even several months after their control littermates did. When injections of testosterone were administered to castrated males, the animals elevated the leg when urinating a few days afterward. Halting the testosterone treatment resulted in a reversion to the puppy urination posture. This was repeated four times in one animal, resulting alternately in leg-elevation and a reversion to the puppy stance during urination. A control over olfaction in one dog did not interfere with the emergence of leg-elevation behavior.

Female sex hormones were injected in large quantities to normal adult males. Instead of disrupting leg-elevation behavior, this treatment initially caused a marked increase in the frequency of leg-elevations, at times more than 100 in an hour. Subsequent smaller injections of estrogens resulted in a disruption of the pattern and a reversion to the puppy urination posture. Cessation of the hormone injections was followed by a revival of normal adult leg-elevation. Male sex hormones injected in female dogs resulted in frequent male copulatory behavior and more frequent urination. However, the adult male leg-elevation pattern did not appear in the females thus treated. Testosterone injected in a young puppy resulted in leg-elevation at eight weeks of age, two months earlier than his control littermates. Partial individuation of the leg-elevation pattern occurred when smaller doses of testosterone were administered to this immature animal. It was also observed that some dogs exhibit a preference when elevating the leg during urination. Evidence from various studies indicates that the neural pattern responsible for copulatory activity in rats is present at birth or shortly afterward. Other evidence indicates that there is a threshold which is lowered or crossed by adequate amounts of the appropriate sex hormone when this neural organization is activated. In order to explain how individuation in canine leg-elevation behavior could occur if the sensori-motor mechanism responsible is present at birth, a hypothesis is advanced which makes use of data from this investigation and other investigations of sex-differentiated behavior. This hypothesis assumes that the sensori-motor mechanism activated by

hormones has several thresholds which when crossed activate portions of the leg-elevation pattern. Thus X amount of testosterone, for example, would cross threshold I and result in the first stage, the gross torsion movement, of leg-elevation. X + Y amount of testosterone would cross thresholds I and II, activating the sensori-motor mechanisms which effect the gross torsion movement and leg-elevation articulated at the hip. X + Y + Z amount of testosterone would cross the thresholds of sensori-motor mechanisms I, II, and III, producing the complete leg-elevation, including crooking the leg.

The data secured from this study are believed to merit the following conclusions:

1. Leg-elevation of adult male dogs during urination is unlearned.
2. A cephalo-caudal direction of development in locomotion precedes leg-elevation in adult male dogs. The leg-elevation pattern follows a proximo-distal direction of development. This pattern is individuated, progressing through readily discernable stages from gross to specific activity.
3. The presence of sex hormones such as testosterone is directly related to the emergence of the leg-elevation pattern in the male dog.
4. Leg-elevation behavior in adult males can be disrupted by treatment with certain female sex hormones.
5. Some dogs reveal a preference as to elevating the right or left leg, at least during the first nine months of life.

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